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What is the temporal extension of edge effects on tree growth dynamics? A dendrochronological approach model using *Scleronema micranthum* (Ducke) Ducke trees of a fragmented forest in the Central Amazon

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ABSTRACT

Although the Amazon Forest comprises the world's largest rainforest, providing fundamental ecosystem services to human well-being, vicissitudes imposed by deforestation, climate change, widespread use of fire and development of new infrastructure make the region critically vulnerable to the consequences of the creation of new forest edges. In this forest fragmentation scenario, temporal assessment of edge effects influences throughout the life of the trees become necessary for a better understanding of how species are affected and react when exposed to altered environments. In this study, we evaluated the temporal influence of the edge effect on the growth dynamics of *Scleronema micranthum* (Ducke) Ducke by tree-ring analysis based on basal area increment and release events. This species is one of the most frequent tree species of terra firme type of forest in Central Amazonia at the Biological Dynamics of Forest Fragment Project (BDFFP) study sites. The results showed that edge effects changed the growth dynamics of the trees for at least 10 years after the disturbance, inducing an 18% reduction in tree growth during this period, and records of increased release events. We concluded that growth rings of edge trees are a valuable bioindicators for evaluating the temporal extent of edge effects, and therefore, they must be considered as relevant ecological indicators of historical environmental changes and forest fragmentation, promoting new insights into the resilience ability of trees when exposed to forest fragmentation processes.

1. Introduction

Amazonia comprises the world's largest rainforest (Wesselingh et al., 2010) providing fundamental ecosystem services to human well-being through supply of essential products and materials, control and support of environmental conditions and the provision of cultural and aesthetic benefits (Millenium Ecosystem Assessment, 2003). However, currently, consequences imposed by deforestation, climate change and widespread use of fire may transform the eastern, southern and central Amazon ecosystem into a non-forest system if deforestation areas cross a tipping point of 20–25% of the region (Lovejoy and Nobre, 2018). In this forest fragmentation scenario, essential ecosystem services provided by trees such as the storage of 60% of the total global forest biomass (Pan et al., 2011), nutrient, carbon and water cycles (Bonan, 2008; Laurance et al., 2018; Spracklen et al., 2012), a source of flowers and fruits (de Groot et al., 2002) and their association with fauna will be affected.

Edge effects that arise as a result of the interaction between habitat and non-habitat areas are corollary to forest fragmentation. Due to the peripheral position to which they are exposed, such areas are the first to receive direct and more intense influences from the external anthropic environment. Such influences can be increasing tree mortality, changing tree community composition, reducing canopy cover, increasing the proliferation of pioneer species, declining the population of hardwood trees and reduction of seedling abundance and survival (Laurance et al., 2006a, Laurance et al. 2006b, Laurance et al., 2000; de Paula

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et al., 2016; Michalski et al., 2007; Bruna, 1999).

Despite the Amazon forest extension, vicissitudes imposed by the main factors of deforestation (e.g. human population density, highways and dry season severity) (Laurance et al., 2002a), make the Amazon forest critically vulnerable to edge effects. Currently, the development of new infrastructure (e.g. hydroelectric dams and roads) would intensify the forest fragmentation (Alamgir et al., 2017; Barona et al., 2010; Fearnside, 2015), expanding the areas exposed to edge effect, as occurred in the Brazilian Amazon, that increased the proportion of forest edge from 10% to 25% (Haddad et al., 2015).

Many studies have evaluated the impact of edge effects on tree composition, recruitment, increment, stem density and mortality of Amazon trees (Sizer and Tanner, 1999; Mesquita et al., 1999; Laurance et al., 2006a, Laurance et al. 2006b, Laurance et al., 2007). However, temporal assessment of the edge effect influences throughout the life of trees become necessary for a better understanding of how individuals of certain species may be affected and react when exposed to altered environments.

In this sense, dendrochronology may be an effective tool for temporal assessing of tree population growth dynamics, reflecting the effect of biotic and abiotic factors on the growth-ring width throughout its life (Babst et al., 2014; Brienen and Zuidema, 2005; Callado et al., 2014; Venegas-González et al., 2018). Moreover, the historical record of growth-rings are able to reveal disturbance events that occurred during the life of the trees (Fraver and White, 2005; Maes et al., 2017), considered discrete episodes in time, that alter the availability of environmental resources and consequently disturb populations, communities and ecosystems (Pickett and White, 1985). The magnitude, timing and duration of those events are usually inferred by growth release (Black et al., 2009), observed in tree-rings as an abrupt increased growth period, sustained over time due to improved light or nutrient condition after mortality of a neighboring tree and a consequent competition reduction (Black et al., 2009; Oliver and Larson, 1996). Such phenomenon may be extended by the new environment and its consequences after the creation of forest edges.

In this study, we used tree-ring lifetime growth patterns, of *Scleronema micranthum* (Ducke) Ducke, Malvaceae, a common tree species (Rankin-de-Mérona et al., 1992), commonly known as "Cardeiro". The specie is considered a canopy tree, rarely semi-deciduous, presenting annual fructification from September to February and flowering from July to October (Alencar et al., 1979). *Scleronema micranthum* trees exposed and non-exposed to edge effects was selected, in order to address the following questions: (i) Are individual growth patterns of trees located closed to a forest edge affected compared with trees located far from the edges?, (ii) What is the temporal extent of edge effect influence on tree growth patterns?, (iii) Are edge effects boosting release events? We believe that tree-rings are important ecological indicators for revealing the setback or progress condition of forest edge effects, promoting new insights on the resilience ability of trees when exposed to a new scenario of forest fragmentation and its edge effects.

2. Materials and methods

2.1. Study and sampling areas

The present study was carried out in the Biological Dynamics of Forest Fragments Project (BDFFP) study sites. The BDFFP can be considered the world's largest and longest-running experimental study of habitat fragmentation (Laurance et al., 2018; Lovejoy et al., 1986) which, since 1979, has been evaluating the impacts of forest fragmentation in the Central Amazon forest (Laurance et al., 2002b). Research conducted earlier at the BDFFP has substantially contributed to our understanding of edge effects (Camargo and Kapos, 1995; Bruna, 1999; Laurance and Yensen, 1991; Laurance et al., 1997, Laurance et al., 2006a; Uriarte et al., 2010). However, evaluating the temporal influence of edge effects on the tree growth dynamics at BDFFP, from a dendrochronological perspective, has not been studied until now, this study being the pioneer in such approach.

The BDFFP is located 80 km north of Manaus, Amazon, Brazil (2°30′S, 60°W), covering an area of ~1000 km^2. A description of the project and the location of all fragments and control areas can be found in Gascon and Bierregaard (2001). The annual precipitation ranges from 1900 to 3500 mm with a moderate, but remarkable dry season from June to October (Laurance et al., 2018).

The phytophysiognomy is predominantly forest, characterized by terra firme type of forest, a term designated for non-flooded Amazon forest (Hopkins, 2005), that represent 80% of the Amazon Biome (Pires and Prance, 1985). Four strata define the forest structure (understory, sub-canopy, canopy and emergent), presenting a 25–35 m canopy on average, with emergent trees that can reach up to 45 m, with at least 1300 species (> 10 cm DBH) (BDFFP personal communication, 2018).

For the present study, two BDFFP reserves were visited to collect wood samples from trunks of *Scleronema micranthum* trees, one of the most abundant and widespread tree species on the study sites (Rankin-de-Mérona et al., 1992). Such abundance allowed us to locate trees exposed and non-exposed to edge effects. Trees exposed to edge effects were located close to the edge or at most, 300 m from any edge in the Porto Alegre farm, specifically at the 100-ha reserve (2°22′2.82″S, 59°58′31.63″W). The reserve was isolated and created in August of 1983, by cutting and burning the surrounding pristine forest to establish new pasture lands. We defined the penetration distance of edge effects up to 300 m because increasing tree mortality associated to forest fragmentation can be detectable until this distance (Laurance et al., 1998). Trees not exposed to edge effects were sampled at Esteio farm, at the continuous forest located within the Km 41 reserve (2°26′15.52″S, 59°46′1.25″W). Trees were located at least 1000 m from the nearest edge (a narrow unpaved road). The reserve was created in 1984, and the forest was kept intact and used as one of the control areas.

2.2. Scleronema micranthum tree-ring analysis

A dendroecological analysis of *Scleronema micranthum* was conducted on 42 adult individuals (≥10 cm DBH), 21 potentially exposed to edge effects and 21 not exposed to any edge effects. The sampled trees were in good phytosanitary condition and did not present liana infestation. Three radial cores were collected for each tree at breast height using increment borers (Diameter = 5.1 mm). Each core was polished with different abrasive sand paper (from 80 to 600 grains/cm^2) with the aim of revealing growth ring boundaries. Subsequently, all tree-rings were identified with the aid of a stereomicroscope according to the classic method (Stokes and Smiles, 1996), using narrow rings as guides. After identification, all tree-ring series was scanned at a resolution of 2400 dpi by an HP G4050 scanner. Measurement of tree-ring width was performed with precision of 0.001 mm through the software Image J.

To evaluate dating accuracy, the temporal series of ring widths were compared within and among trees at each site. Both visual and statistical cross dating were performed. Visual cross dating was done working with ring-width bar plots, and statistical cross dating was tested using COFECHA software (Holmes, 1983). COFECHA uses segmented temporal series correlation techniques to assess the quality of cross dating and measurement accuracy in the growth ring time series (Grissino-Mayer, 2001).

After evaluating the dating in COFECHA software, we sought to construct master chronologies for each site that would increase the retention of common growth signals. According to Cook and Kairiukstis (1990), spline functions with length between 67% and 75% of the series are able to remove biological growth trends related to high frequency variances. To build site chronologies, time series were detrended and standardized using a smoothed cube spline function with 50%

frequency-response cut-off for 65% of the length of each series in dplR package in R Software (Bunn, 2008). The standardization of the series is performed by dividing the width of the growth ring by the growth model of the smooth cubic spline function, producing dimensionless ring-width indices (RW) (Bunn and Korpela, 2017). The quality of the chronology was evaluated by the value of Rbar and EPS (expressed population signal), both calculated with the dplR package on R Software (Bunn, 2008). The Rbar is the average correlation coefficient resulting from comparing all possible segments of a predetermined length among all the series included in the chronology (Briffa, 1995). The EPS values provided information that confirmed the existence of common signals among trees, EPS values higher than 0.80 indicate that the limiting factor to growth in the chronology probably is homogenous (Mendivelso et al., 2014).

2.3. Site growth patterns

To explore growth patterns among trees located close to the edges and trees located in the interior of the forest, width of the growth rings was converted into basal area increment (BAI). BAI is considered a more informative measure of tree growth trends in terms of total biomass production (Peñuelas et al., 2011; Phipps and Whiton, 1988) and decreasing tendency will only be presented in senescent trees or when trees are subjected to significant growth stress (Duchesne et al., 2003; Jump et al., 2006). The width of the growth ring was converted to BAI according to the following standard formula: $BAI = \pi (R^2n - R^2n-1)$, where R is the tree radius and n is the growth ring formation year. To calculate BAI we used the bai.out function in dplR package in software R (Bunn and Korpela, 2017; Bunn, 2008).

Principal Component Analysis (PCA) was performed to identify dominant BAI patterns between edge and interior trees during common growth periods: all periods (1941–2014), before edge creation (1941–1982), five years after edge creation (1983–1987), ten years after edge creation (1983–1992) and fifteen years after edge creation (1983–1997). The PCA was realized by the prcomp function in R software (R core Team, 2017). The use of PCA to detect growth patterns is widely employed in dendrochronological studies (Oliveira et al., 2010; Rodríguez-Catón et al., 2016; Venegas-González et al., 2017; Villalba et al., 1998) and by reducing the dimensionality of multivariate data, it supports the results interpretation (Legendre and Legendre, 2012). Through the data dimension reduction, the PCA automatically performs data clustering according to the K-means objective function (Ding and He, 2004). Thus, seeking cluster validation of trees exposed and unexposed to edge effects, Silhouette Index (SI) (Rousseeuw, 1987) was used. The SI evaluates how much a sample is similar to another inserted in the same cluster, comparing with samples inserted in other clusters (Kaufman and Rousseeuw, 2009). SI values near +1 indicate that the sample is far from the neighboring clusters, confirming that the sample was correctly allocated. A value of 0 indicates that the sample is very close to the decision boundary between two neighboring clusters, and negative values indicate that sample might have been assigned to the wrong cluster (Rousseeuw, 1987). After PCA, we used one-way ANOVA with Tukey's post hoc test ($p < 0.05$) to compare BAI trends between edge and interior clusters.

2.4. Disturbance analysis

Some of the most widely used methods for identifying release events are radial growth averaging techniques, in which a growth change percentage (%GC) calculation is made on each tree ring time series, and release events are recorded when growth change percent values exceed a certain minimum value (Black et al., 2009; Nowacki and Abrams, 1997). In this way, to detect release events we used the formula of Nowacki and Abrams (1997) to derive the growth change percentages: $\%GC = [(M2 - M1)/M1] \times 100$, where %GC = growth change percentage for year 1, $M1$ = mean diameter growth over the preceding 10 years, and M2 = mean diameter growth over the subsequent 10 years. Studies in tropical forests reveal that a moving average of 10 years was able to remove long-term age-effects and short-term climatic fluctuations (Brienen et al., 2010; Brienen and Zuidema, 2006; Rozendaal et al., 2011). Release events were identified when the %GC was greater than 50% during a minimum period of 10 years (Rozendaal et al., 2011). Release events were performed by overall function by the Nowacki and Abrams (1997) method using the "TRADER" package (Altman et al., 2014) in R (R core Team, 2017).

Seeking to verify if the %GC that promoted release events before and after the edge creation induced statistically significant differences in the wood production, one-way ANOVA with Tukey's post hoc test ($p < 0.05$) was performed on the growth changes of BAI (ΔBAI). ΔBAI was calculated as the difference in the BAI average ten years before the release events and ten years after the release events. ANOVA was performed by the OAV function in R software (R core Team, 2017).

3. Results

3.1. Tree-rings chronologies of Scleronema micranthum

The growth rings of *Scleronema micranthum* trees at both sites were distinct and characterized by tangentially distended rays touching the apotracheal, possibly terminal parenchyma bands (Vetter and Botosso, 1989a) (Fig. 1).

The master chronology (Fig. 2) was built from tree-ring widths covering 138 years (1878–2015) for trees located within the interior of the forest and 142 years (1874–2015) in trees located close to the edges,

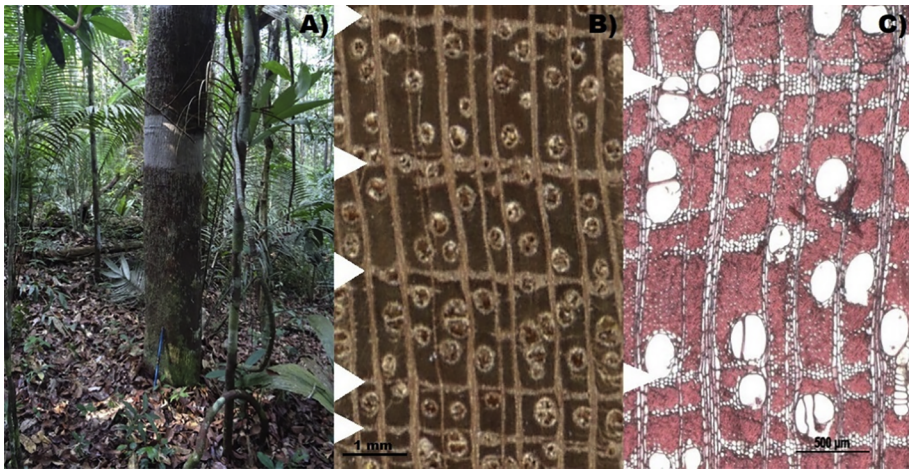

Fig. 1. a) *Scleronema micranthum* tree on edge at Biological Dynamics of Forest Fragments Project site; b) Macro and c) microscopic images of the transverse wood section evidencing the growth ring anatomy characterized by tangentially distended rays touching the apotracheal, possibly terminal parenchyma bands. White triangles indicate the growth-rings limits.

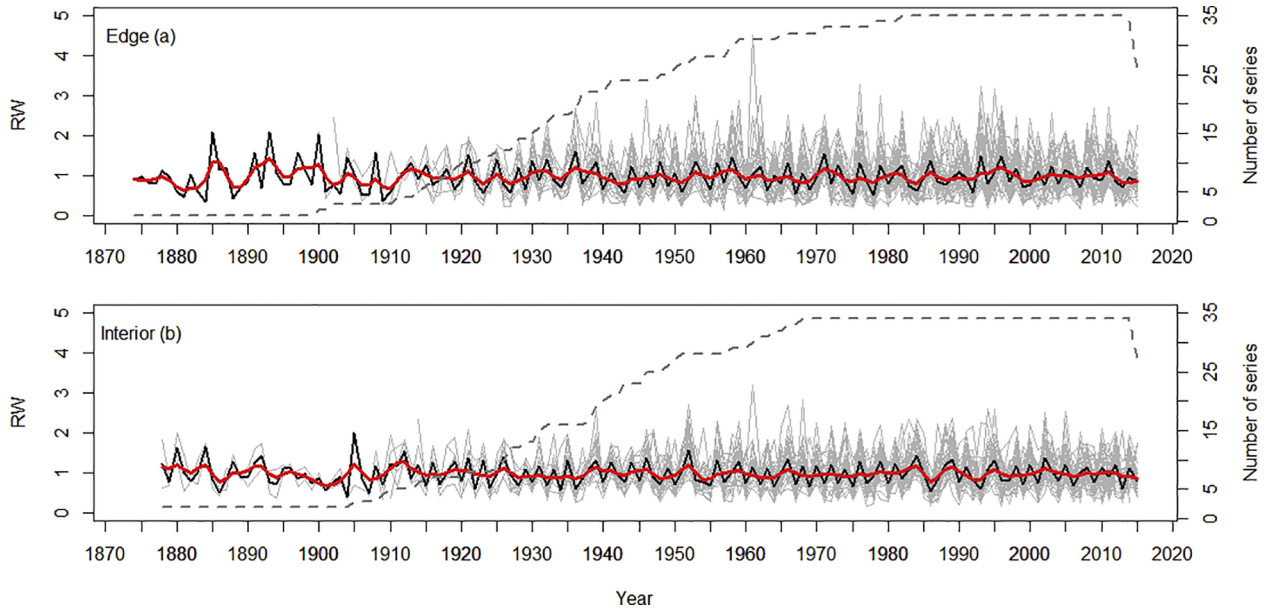

Fig. 2. Residual tree-ring chronology of *Scleronema micranthum* trees for Edge (a) and Interior (b) locations in terra firme type of forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia. Grey solid line: individual average time series; black line: residual tree-ring master chronology; grey dotted line: number of series used for the index calculation; red line: standardization of master chronology by a 10% smoothed spline curve. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Descriptive statistics of the chronologies of *Scleronema micranthum* trees located close to the edge and in the interior of the reserve at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.

Variables	Edge	Interior
No. trees/No. radial cores	21/34	21/34
Mean ring width ± s (cm)	0.18/0.12	0.18/0.09
Time span	1874–2015	1878–2015
Age ± s	81/22	81/22
Mean sensitivity	0.56	0.51
Series intercorrelation	0.51	0.50
Rbar (± s)	0.4/0.02	0.3/0.05
Period with EPS ≥ 0.80	1920–2015	1915–2015

confirming the presence of trees all over the forest far before isolation and creation of the reserve in 1983. The cross-dating quality and accuracy in the measurements of the growth rings was confirmed by the correlations, EPS > 0.80 and Rbar > 0.3 values, indicating a common growth pattern of *Scleronema micranthum* at each site. The descriptive statistics of the chronologies are presented in Table 1.

3.2. Site growth patterns

After the construction of the chronologies and the growth-ring annuity confirmation, we sought to compare edge and interior population growth patterns with similar age and diameter structure. For this, 15 trees located close to the edge and 15 trees located in the interior of the forest representing age and diameter corresponding population structure of a common growth period (1941–2014) were selected (Table 2).

Principal component analysis (PCA) over a common growth period (1941–2014) (Fig. 3a) revealed that trees closed to the edge and in the interior of the forest shared basal area increment (BAI), a common sign retained mainly by the Axis 1, responsible for 43% of the data variance and, a more divergent growth signal retained by Axis 2 and responsible for 10% of the variance. The formed clusters presented a weak silhouette coefficient (< 0.5), confirming BAI patterns homogeneity throughout the 73 years analyzed.

When performing PCA before forest fragmentation and edge creation (1941–1982) (Fig. 3b) we observed that the BAI variance retained by component one increases (47%) and the variance retained by component two decreases (9%). Although the variance retained by Axis 1 and 2 in PCA prior to edge creation are close to the observed in the whole analyzed period (Fig. 3a), the non-validation of the cluster by the Silhoute index (< 0.2), and the lack of statistically significant differences between BAI series through ANOVA ($F = 0.58$, $p = 0.44$), confirm that previously forest fragmentation, trees located close to the edge (4.90 cm^2, SE = 0.20) and within the forest interior (4.69 cm^2; SE = 0.17), presented higher homogeneity in their BAI dynamics.

Table 2
Age and diameter at breast height (DBH) of *Scleronema micranthum* trees at edge and interior sites in Terra Firme Forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia selected for growth pattern analyzes.

	Edge		Interior	
Year	DBH	Age	DBH	Age
1941	6.9 (s = 5.8)	20 (s = 17)	6.9 (s = 6.2)	23 (s = 18.2)
1982	22.3 (s = 6.3)	61 (s = 17)	22.1 (s = 7.1)	64 (s = 19)
2014	33.3 (s = 5.2)	92 (s = 17.8)	34.9 (s = 6.7)	96 (s = 12.2)

Although similar BAI patterns are shared (Fig. 4), major tendency differences are observed from 1972 to 1990. Before forest fragmentation (1972–1982), BAI divergences among trees located close to the edge (4.90 cm^2; SE = 0.51) and in the forest interior (4.69 cm^2; SE = 0.42), were not statistically significant according to ANOVA ($F = 0.003$; $p = 0.95$). We can observe in Fig. 4 that the divergences occurred before forest fragmentation promoted differences mainly in the BAI amplitude. However, after forest fragmentation, BAI trends were altered, opposing patterns of increase and reduction occurring in wood production within the populations separated by the new environmental conditions promoted by the forest edge. Nonetheless, when we performed the variance analysis ($F = 3.27$, $p = 0.07$) after forest fragmentation (1983–2014), edge (15.36 cm^2; SE = 0.6) and interior trees (14.07 cm^2; SE = 0.4) still did not present statistically significant differences among BAI series. Thus, we assume that: i) edge effects did not alter the growth dynamics of the trees or ii) edge effects were

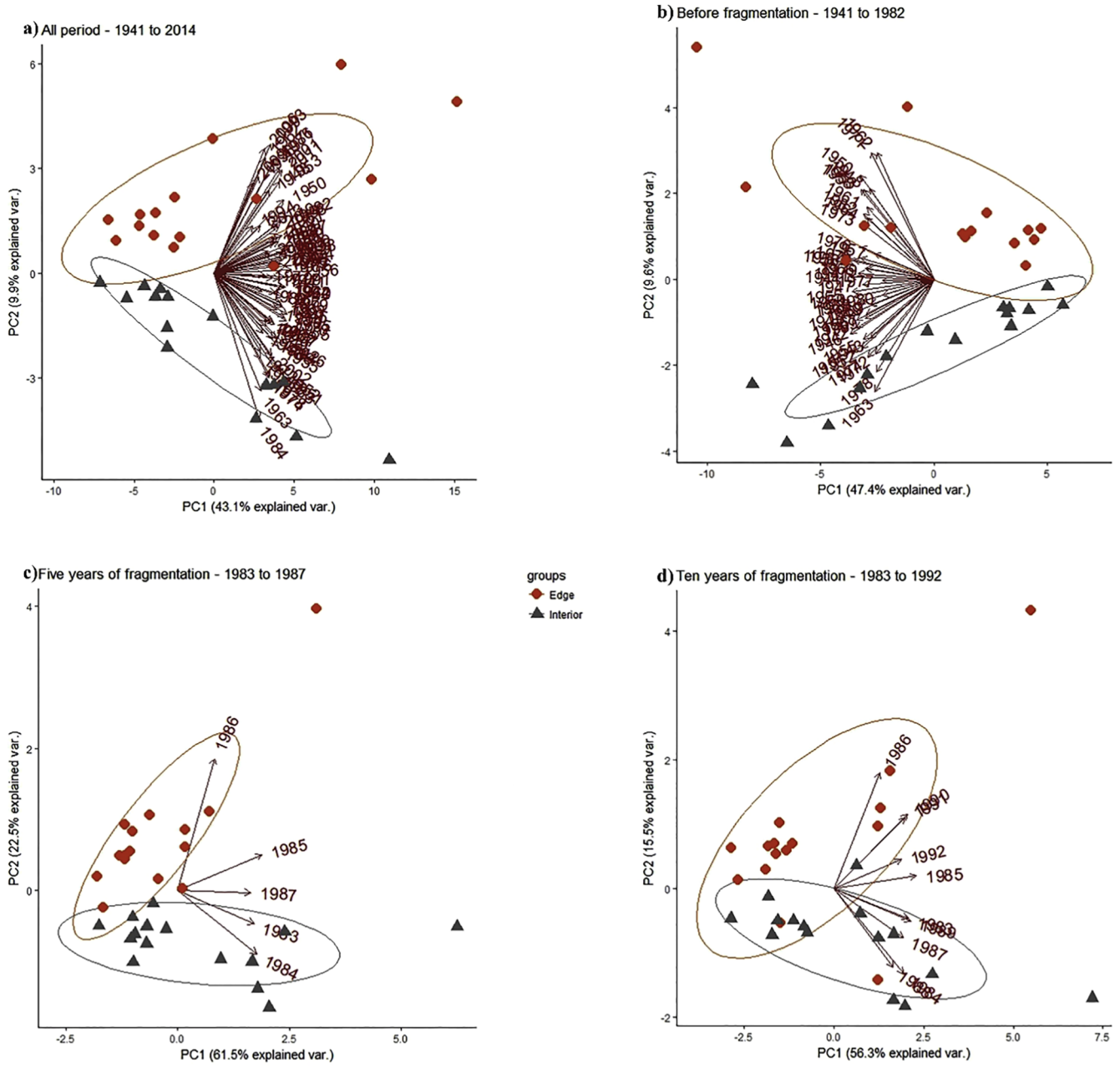
a) All period - 1941 to 2014
PC2 (9.9% explained var.)
PC1 (43.1% explained var.)
b) Before fragmentation - 1941 to 1982
PC2 (9.6% explained var.)
PC1 (47.4% explained var.)
c) Five years of fragmentation - 1983 to 1987
PC2 (22.5% explained var.)
PC1 (61.5% explained var.)
groups
Edge
Interior
d) Ten years of fragmentation - 1983 to 1992
PC2 (15.5% explained var.)
PC1 (56.3% explained var.)

Fig. 3. Principal Component Analysis described by BAI series of *Scleronema micranthum* trees located close to the edge (orange circles) and in the interior of the forest (gray triangles) in terra firme type of forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

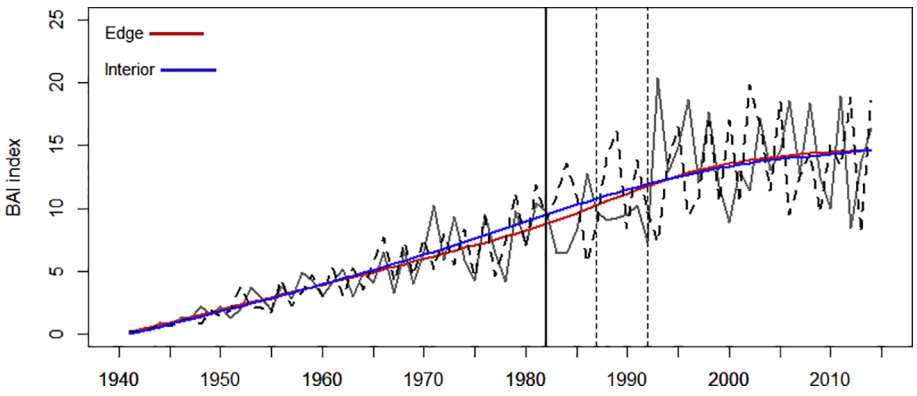

Fig. 4. Dominant basal area increment (BAI) index patterns of *Scleronema micranthum* trees located close to the edge (grey solid lines) and in the interior of the forest (black dashed line) in terra firme type of forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia. Red line: Standardization by a 30% smoothed spline curve of BAI chronology of trees located close to the edge; blue line: Standardization by a 30% smoothed spline curve of BAI chronology of trees in the interior of the forest; vertical black solid line: edge creation year (1982); vertical black dashed line: five and ten years after edge creation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

temporal, reducing the intensity during the 73 years evaluated.

Our results identified the temporality of edge effects in the growth rings of *Scleronema micranthum* trees mainly in the first 10 years after edge creation. During the first five years (1983–1987) ordination analysis showed that the intensity of edge effects was strong enough to cluster edge and interior trees through the second main component, responsible for 22% of the data variance (Fig. 3c). Silhouette coefficient > 0.7 supported the ordination. The variance increase retained by component two demonstrates the strength increase of the most divergent BAI signal during the first five years of forest fragmentation and edge creation. In trees located close to the forest edge the result reflected 22% lower wood production during this period, statistically supported by ANOVA ($F = 3.34$, $p = 0.04$). However, the retention of 61% of the data variance by component one still indicates the sharing of common growth signs between edge and interior trees during the first five years of edge creation.

When performing the PCA for 10 years after edge creation, we verified that the intensity of the effects that ordered the clusters was reduced to 15% of the variance (Fig. 3d), indicating a strength reduction of the most divergent BAI pattern, related to edge effects. Despite the lower strength, the cluster ordination was supported by the silhouette coefficient (=0.5). The edge effects influenced during the first 10 years resulted in 18% lower wood production (10.4 cm^2; SE = 0.58) for trees closed to the edge, compared to those of the interior (12.31 cm^2; SE = 0.60), data supported by ANOVA ($F = 5.38$, $p = 0.02$). From the tenth year, BAI differences were not statistically significant by analysis of variance and principal components, presenting non-validated clusters by the Silhouette coefficient < 0.4. Table 3 presents the BAI of trees located close to the edge and in the interior of the forest during the analyzed time periods.

3.3. Disturbance analysis

Disturbance analyses were able to detect differences in growth release events between trees exposed and non-exposed to edge effects (Fig. 5). In general, during the evaluated period of 73 years, 47 growth release events were observed in trees located close to the edge, 31 of those events occurred after forest fragmentation and only half of them (16 in total) occurred before the edge creation. About 65% of major events occurred after forest fragmentation and edge creation. Analysis of variance confirmed that the BAI growth changes (ΔBAI) after forest fragmentation (ΔBAI = 7.05 cm^2; SE = 1.0) was, on average, 50% higher than those occurred prior to forest fragmentation (ΔBAI = 4.69 cm^2, SE = 0.8). However, ANOVA analyses do not confirm greater differences in the first five and ten years after edge creation.

Trees located close to the edge presented an average diameter at breast height (DBH) of 19 cm (s = 6) in the years of release events that occurred before edge creation, and 24 cm (s = 5) DBH in the years of release events that occurred after forest fragmentation. Indicating that in the years of release events, the trees occupied the forest canopy or were close to it.

Trees not exposed to edge effects presented 50 release events over the 73 years evaluated (1941–2014). In the release year 56% of the interior trees had an average DBH of 13 cm (s = 3), indicating a subcanopy position in the forest vertical profile. This is the opposite of that observed in the previous group of trees that occupied, in most release events, a position in the forest canopy.

Although the number of release events after edge creation is greater in trees close to the edge, they did not result in statistically significant differences in ΔBAI within individuals located close or far from the edge, in the first five, ten and fifteen years after forest fragmentation. Thus, results indicated that disturbances caused by edge effects are inducing an increased number of growth release events in *Scleronema micranthum* trees, but not necessarily increasing ΔBAI compared to the trees located far from the forest edge.

4. Discussion

4.1. Tree-ring chronologies of Scleronema micranthum trees

The *Scleronema micranthum* dendrochronological potential has been recognized since the pioneering works of Vetter and Botosso (1989a,b, 1988) which confirmed, through anatomical structures, climatic relationships and incision in the vascular cambium (Mariaux window), the growth ring annual formation. The high value of correlation, EPS and Rbar reached by the edge and interior chronologies, is strong evidence that the growth rings are indeed synchronized with the annual calendar, proving the existence of a common sign among trees (Briffa, 1995; Stahle, 1999).

The annual dry season present in the region from July to September with a monthly precipitation near 60 mm should be a growth limiting factor (Stokes and Smiles, 1996) capable of inducing a seasonal rhythm of wood formation (Worbes, 1995), and therefore the existence of annual growth rings in *Scleronema micranthum* trees.

4.2. Site growth patterns

Growth rings demonstrated to be quite valuable archives of the annual variability of tree growth (Babst et al., 2014; Brienen et al., 2016), providing, through an annual dimension, a great refinement in studies of forest dynamics (Biondi, 1999) and specifically, as focused on in our study, a refinement in studies on edge effects after forest fragmentation. Mainly through PCA and ANOVA results there was indication of the return of a common growth pattern between trees located close to the forest edge and within in the interior of the forest only after 10 years of forest fragmentation. This revealed that edge areas, besides losing significant amounts of biomass via mortality of large trees during the first five years of forest fragmentation (Laurance et al., 2007), can continue to affect the basal area increment dynamics of the surviving trees for at least another 10 years. According to Stephenson et al. (2014), old survival trees do not act simply as senescent carbon reservoirs, but actively fix large amounts of carbon compared to smaller trees. Thus, the BAI reduction of surviving trees during the first 10 years of edge creation, probably can also reduce the carbon stock potential of old trees in fragmented areas.

Table 3
Basal area increments (BAI) of *Scleronema micranthum* trees located close to the edge (Edge BAI) and in the interior of the forest (Interior BAI) during a common growth time period in Terra Firme Forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia. The asterisk indicates the statistically significant differences by one-way ANOVA with Tukey's post hoc test ($p < 0.05$).

	Edge BAI	Interior BAI
All periods – 1941 to 2014	9.42 cm^2, SE = 0.32	8.75 cm^2, SE = 0.23
Before forest fragmentation – 1941 to 1982	4.90 cm^2, SE = 0.20	4.69 cm^2, SE = 0.17
After forest fragmentation – 1983 to 2014	15.36 cm^2, SE = 0.60	14.07 cm^2, SE = 0.40
Five years of forest fragmentation – 1983 to 1987	*9.62 cm^2, SE = 0.71	*11.81 cm^2, SE = 0.93
Ten years of forest fragmentation – 1983 to 1992	*10.36 cm^2, SE = 0.58	*12.31 cm^2, SE = 0.60
Fifteen years of forest fragmentation – 1983 to 1997	12.98 cm^2, SE = 0.67	12.33 cm^2, SE = 0.49

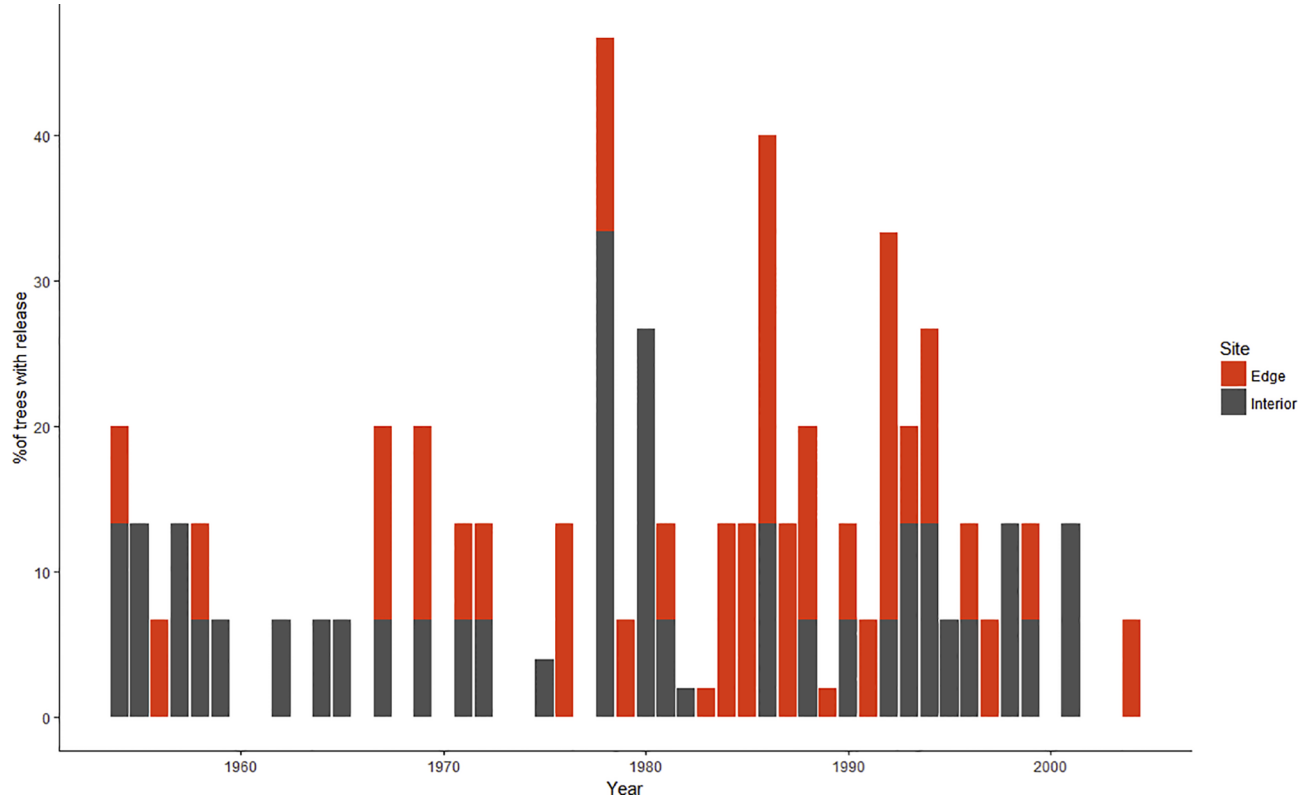

Fig. 5. Release events in *Scleronema micranthum* trees close to the forest edge (orange) and in the interior of the forest or far from the edge (gray) in terra firme type of forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

After forest fragmentation, the carbon reservoir role is redistributed within the trees and in the first years of restoration is mainly associated with the growth of early-successional species. During the last stages of succession, the slow growing trees will contribute more significantly (Shimamoto et al., 2014). This result reflects the increased tree mortality (Laurance et al., 2006a, Laurance et al., 1998) and elevated photo-synthetically active radiation (PAR) caused by lateral light penetration from the nearby clearing (Sizer and Tanner, 1999) that favored an increase in the diameter increment in early-successional species (0–50 cm DBH) (MCDonald and Urban, 2004). Surveys in BDFFP study sites proved that faster-growing species have increased density and basal area increments in the forest edge, favored mainly by the stand-level tree mortality and the number of nearby forest edges, shifts that can become even more abundant over time (Laurance et al. 2006b). Simultaneously, many slow-growth tree species are disfavored by the new environmental condition, and eventually may be driven to local extinction (Michalski et al., 2007). In undisturbed forests at the BDFFP, Laurance et al (2004) revealed, for a period of 15 years, a tendency for canopy and emergent trees to increase in population density and basal area compared to small trees and justifies that the most likely cause of higher productivity in undisturbed Amazon forest is because of rising atmospheric CO_2 levels.

However, for disturbed Amazon forest, our dendrochronology approach revealed that the consequences can be distinct. We identified, that late-succession trees, such as *Scleronema micranthum* (Marenco and Vieira, 2005), when remaining in edge areas after forest fragmentation, can present a lowest basal area increment in the first 10-year period. In other words, edge effects may reduce canopy tree productivity for a least 10 years. In reserves of 1 ha (highest forest/edge ratio) at the BDFFP, *Scleronema micranthum* trees fructify outside the period normally expected for the species (September–February) and reduce the flowering period, indicating a probable disturbance in the flower and fruit production process in fragmented areas (Rankin de merona and Ackerly, 1987), results associated to reduced productivity that can alter their ecosystem services.

By occupying a canopy position in the year of edge creation, *Scleronema micranthum* tree crowns are exposed to intense sunlight and evapotranspiration. Thus, knowing that large tropical trees are vulnerable to droughts (Condit et al., 1995), this late-succession tree species can be more sensitive to a desiccation increase (Kapos, 1989) in edge areas. As such, it is believed that the micro-climatic changes, such as elevated temperatures, reduced humidity and increased vapor pressure deficits, occurring in newly created edges lead to depleted soil moisture, creating drought stress (Camargo and Kapos, 1995; Malcolm, 1998; Pinto et al., 2010; Sizer and Tanner, 1999). This situation may have influenced the lower wood production in *Scleronema micranthum* trees mainly after the first ten years of edge creation. These are results which, added to the expected temperature increase due to climate change (Allen et al., 2015), can have important consequences for trees exposed to the edge effects. The resumption of the more homogeneous BAI pattern after 10 years reflects the edge evolution phases, which after five years of forest fragmentation, presented greater stability in the edge-related changes favored by the progressive growth of secondary vegetation that seals the edge (Camargo and Kapos, 1995; Harper et al., 2005). Although edge effects can be considered one of the main drivers of ecological change in the BDFFP fragments, at least over the first 3–4 decades after edge creation (Laurance et al., 2018), the dendrochronological approach identified major influences on the *Scleronema micranthum* tree BAIs during the first 10 years of forest fragmentation and edge creation. Thus, we can consider the secondary forest that regenerated after forest fragmentation as a facilitator of the resumption of the common growth pattern for the *Scleronema micranthum* trees exposed to edge effects, corroborating with the classical ecological theory of Clements; that of a superorganism that recovers and adjusts after undergoing some sort of impact. In this way, we highlight the importance and necessity of preservation of secondary

forests after forest fragmentation processes for the maintenance of impacted areas, as areas under edge effects.

4.3. Disturbance analysis

A release event is identified in the growth rings as a period of sudden increase in growth over time (Nowacki and Abrams, 1997). These events can be associated with increases in light or water availability following a disturbance that removes or reduces surrounding competitors (Black et al., 2009; Brienen and Zuidema, 2006; White and Pickett, 1985). Edge areas are recognized by increased light incidence (Camargo and Kapos, 1995; Lovejoy et al., 1986; Williams-Linera, 1990) and tree mortality (Laurance et al., 2000; McDowell et al., 2018; Mesquita et al., 1999), favoring release events in trees close to forest edge after edge creation.

By identifying that trees exposed to edge effects exhibit a greater number of release events, disturbance analyzes admit that edge effects induce tree growth increase (Harper et al., 2005). This result appears to be opposite to that observed in the analysis of growth patterns that proved, during the first 10 years of forest fragmentation (1983–1992), a lower BAI in trees located close to edges compared to the trees in the interior of the forest. However, when we analyzed only the trees located close to the edge we observed that release events after forest fragmentation really induced 50% greater ΔBAI in relation to events prior to edge creation. That is, release events after forest fragmentation promoted higher growth changes in edge trees than those that occurred prior to fragmentation, although this difference does not reflect higher growth in relation to interior trees.

The vertical light gradient created by the forest canopy represents the greatest challenge for tree establishment, particularly canopy trees (Harcombe and Marks, 1978). Consequently, in order to reach the forest canopy, saplings of many species require periods of increased light (areas close to gaps) (Brokaw, 1985; Yamamoto, 2000). Hence, trees that do not occupy a canopy position are expected to exhibit larger release events (Brienen et al., 2010; Rozendaal et al., 2011). However, our study revealed that release events in edge areas that promoted higher ΔBAI were performed by *Scleronema micranthum* canopy trees after forest fragmentation. This could indicate release advantages in canopy trees that survived to edge creation, increasing the competition for sunlight capture, what could harm the canopy ascension in trees of lower strata, changing the forest dynamics. However, when surviving trees are infested by lianas, the leaf shading of the phorophyte may reduce the growth rates and the number of release events in trees exposed to edge effects, as observed in *Aspidosperma polyneuron* trees in the Brazilian Atlantic Rain Forest (Godoy-Veiga et al., 2018). These results are not observed in our study due to the absence of liana infestation in *Scleronema micranthum* trees, evidencing more strongly the edge effect as an important (and temporary) factor of systemic imbalance.

Through the disturbance analysis, we identify the hyperdynamic tendencies in fragmented areas (Laurance, 2002; Laurance et al., 2018), reflecting the release event frequency increase and ΔBAI amplitude increase after edge creation. The hyperdynamism in fragmented areas can have serious ecological impacts, altering disturbance regimes, mortality and recruitment and turnover rates, population fluctuations of individual species, species local extinction, and the pace of biogeochemical cycling (Laurance, 2002). However, the return to the more homogeneous BAI pattern between edge and interior location and the presence of only six release events in trees located close to the forest edge after 10 years of fragmentation may indicate that the hyperdynamic tendency of *Scleronema micranthum* growth may gradually stabilize and approach the pre-fragmentation condition after 10 years of edge creation. However, considering that fragmented areas are more susceptible to stochastic events (de Paula et al., 2016), the temporality of the hyperdynamic condition may be extended even longer.

5. Conclusions

Through the growth-ring analysis we revealed that the edge effects on terra firme type of forest in Central Amazon are changing the growth dynamics of the *Scleronema micranthum* trees for at least 10 years after edge creation, inducing an 18% reduction in tree growth in this period. The resumption of the more homogeneous BAI pattern between trees located at the edge and in the interior of the forest after 10 year of edge creation proves the temporal extension of edge effects, presenting greater stability in the edge-related changes favored by the growth of secondary vegetation that progressively seals the edge or at least diminishes its effects. The increase in release events after edge creation reflects the hyperdynamic condition of fragmented areas, although this result does not manifest itself in greater growth in relation to trees not exposed to edge effects. This study demonstrates the potential of tree ring analysis in evaluating the temporal extent of edge effects, promoting a future perspective of management and forest conservation. We therefore emphasize the potential and importance of considering growth-rings as relevant ecological indicators of historical environmental changes associated with forest fragmentation.

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